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Notes on the Courtship Behavior of the Blue-backed Manakin (*Chiroxiphia pareola*)

BY E. THOMAS GILLIARD

Manakins are sparrow-sized Neotropical birds. As a result of convergent evolution, many employ patterns of behavior that resemble those of the grouse and birds of paradise. As are their large counterparts, many of the 59 species forming the Pipridae are highly dimorphic, having specialized ornamental plumage on the head, throat, wings, and tail, and special structural modifications for the mechanical production of sound. As do the males of grouse and birds of paradise, many of the manakins display on special stages or bowers. Some perform solitarily, away from other males; others perform in loosely interacting groups, with each male occupying and defending a private display stage; and in a few species, such as the one reported upon herein, groups of males gather to dance highly ritualized dances (i.e., to render specialized, generally exaggerated, visual and auditory signals designed to attract the female), involving synchronized performances in which pairs or groups of males take part.

The display stages of the various polygamous manakins are located on the ground, in low branches, or on slender limbs that may be in the middle tier of the forest or high up in the crown. The males spend much time in these "bowers," cleaning them of fallen debris if they are ground stages, plucking leaves around them if they are arboreal stages, and of course dancing in them. During these intervals they are exposed to unusual predatory pressures from lizards, snakes, mammals, and birds, which quickly learn the locations of the dancing stages.

The biological advantages of these forms of reproductive behavior, with their seemingly excessive exposure to predatory pressure, are still obscure, and they must remain so until the various types have been adequately studied.

With this thought in mind, the following field observations of *Chiroxiphia pareola* are offered. The field work was done during the course of an expedition to Little Tobago, sponsored by the National Geographic Society and the American Museum of Natural History, to study an introduced breeding population of Greater Birds of Paradise (*Paradisaea apoda*). Following completion of that work, I went to northern Tobago Island to observe a clan of Blue-backed Manakins that the camp cook, Latimer Spencer, said had been dancing each dry season for decades in a gorge near his home. Fifteen minutes after I first entered the gorge, I observed a pair of Blue-backed Manakins performing an aerial dance in which they resembled two colorful balls being juggled rapidly. This, together with a buzzing accompaniment, continued for about a minute. Immediately thereafter I built a blind of a green tarpaulin camouflaged with leaves.

From this structure observations were made on March 16 (approximately 4.15 P.M. to 5.45 P.M.), March 17 (5.50 A.M. to 4.45 P.M.), March 18 (6.01 A.M. to 1.50 P.M.), and March 19 (approximately 7.45 A.M. to 8.00 A.M.). All observations were immediately recorded, together with field sketches and maps. The most important of these are recorded in detail below in this paper. In this connection it is important to note that I had no prior knowledge of the behavior of this species; specifically, I had not seen either Snow's account of its dances (1956) or Slud's report (1957) on the nearly related *C. linearis*.

Chiroxiphia pareola is one of the most colorful manakins. The size of a sparrow, the adult male has the back pale cerulean blue and the crown glossy red. Elsewhere it is velvety black. In life the legs are light yellow, and the iris is brown. The outer primaries are narrow and rigid, with the outer vanes very narrow and jagged in appearance. The adult female is yellowish olive above, becoming much paler and more grayish below, especially on the abdomen, which is washed with pale yellow. It has the primaries somewhat less rigid than those of the male. The immature male is colored like the female, but it has the crown bright red and the flight feathers as in the adult male. The very young male is probably indistinguishable from the adult female. These plumages permit an unusually wide degree of identification in the field, because (a) the adult male (red and blue) is always unmistakable; (b) the subadult male (red and green) is always unmistakable; and (c) the female (green) is identifiable (except from the first-year male).

It is fortunate that the colors are so definitive because of the confusing diversity of the behavior, particularly that involving males of different age groups. Otherwise the patterns of courtship behavior would be infinitely more difficult to solve, for it would be necessary to collect interacting birds in order to determine their sexes, as, for example, Rand (1940, p. 6) had to do in *Macgregoria pulchra*. Indeed, in species of manakins in which the subadult males are indistinguishable from the females, it is probable that observers who fail to collect some of the interacting pairs are not able to solve the complexities of their displays.

Another problem is the need of many observations in order that the behavioral variability of a species may be plotted and thus permit diagnostic patterns to be unmasked. For example, in the species under consideration here, D. W. Snow (1956, p. 89) observed that the males kept together in pairs and that these "pairs of males appear to occupy fixed territories in the forest; they spend much of their time together and . . . nearly all of their displays are performed jointly." Snow also noted that the pairs always uttered certain calls when sitting together (p. 90) and that after thus calling the pair often moved down to their display perch. The population reported here, living less than 5 miles from that studied by Snow, showed quite a different pattern of behavior. The specific territories appeared to be occupied not by specific pairs but by a mixed group of males, which interacted by dancing (one at a time) with many partners of varying ages, in any of the four dance territories comprising the general arena. Furthermore, coordinated dancing by a pair of males was observed to occur without apparent preparation or conditioning other than general disturbances, such as men walking through the woodlands or the sound of chopping. It also took place as the climax of a group dance in which as many as four or more males joined together in a single "bouncing" display.

ECOLOGY

Local informants reported that display areas of the Blue-backed Manakin were not uncommon in northern Tobago Island. The area chosen for this study was approximately 1 mile northwest of Speyside, on the northwest side of Batteaux Bay Ridge, about 200 feet below and 600 feet roughly west of a moss-grown, coffin-shaped marble crypt on which was engraved the date July 14, 1808, and the name Isabella Lidgerton. The "bower" area was in a dry draw situated between two low ridges. This draw and the ridges were moderately forested with old second-growth trees, some of them 70 feet in height. The lower tier of this forest was composed of bushy trees and small saplings. Visibility

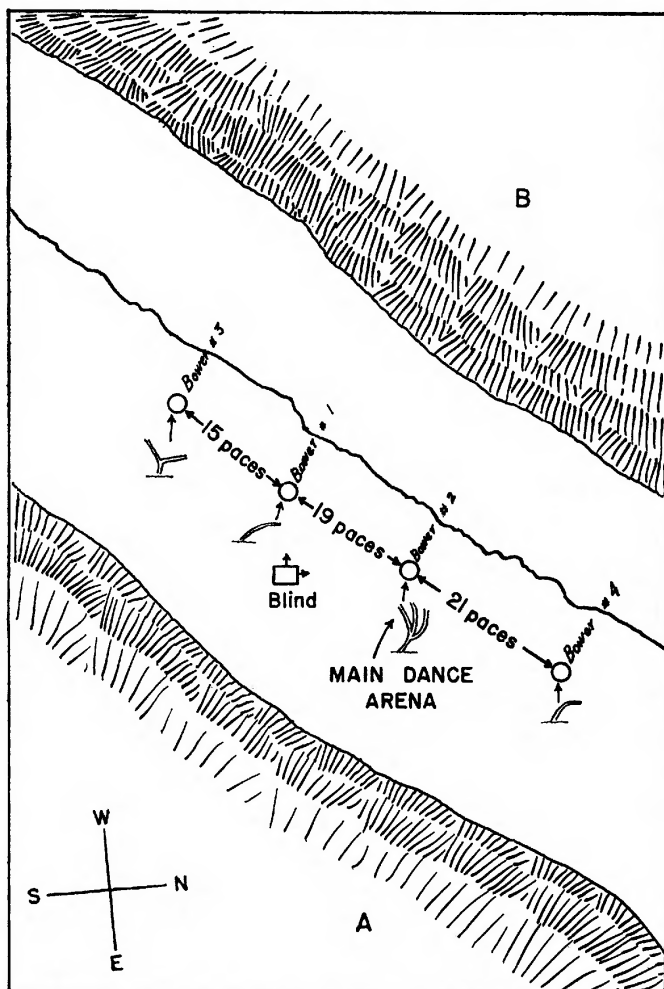


FIG. 1. Dance arena of *Chiroxiphia pareola*. Arena consisted of a main bower (2) and three auxiliary bowers (1, 3, and 4). Bowers are numbered in order of discovery.

was good until about 3.00 P.M., when the western heights of Pigeon Peak began to screen the setting sun. Through this shallow draw, which was about 100 feet wide, a stream bed (dry at the time of my visit) drained towards the southwest. Situated parallel to this water-course were four bowers, which were observed to be constantly used as dancing stages by *C. pareola*. These were spaced 15, 19, and 21 paces apart, in a nearly straight line (fig. 1). All were in more or less

the same type of open bushy forest, 25 to 60 feet south of the stream bed. These stages were discovered one by one as the birds went to them to dance, and the numbers assigned to them indicate their order of discovery. They consisted of slender perches close to the ground, as follows:

Bower 1 was a slender shaft sloping steeply upward. The center of this dance stage was 29 inches above ground, and the shaft used for dancing extended from about 26 to 32 inches above the ground. Although several other perches in the vicinity were used for sitting, dancing was observed only on and above the nearly vertical shaft. Many observations of adult and immature males dancing together were made at this display ground. Color motion-picture films and stills of "cartwheeling" males were exposed at this stage.

The second bower to be discovered proved to be the one most frequently used. It consisted of a number of thin, nearly horizontal perches and several towering shafts. The main dancing spot in this bower was about 36 inches above the forest floor on a nearly horizontal perch. Many secondary perches were located on each side of the main stage. In this display arena groups of four males were seen dancing together like so many alternately bouncing balls, and it was here that cartwheeling pairs of males were approached by other males, and sometimes three males danced in a single reel as one "cut in" on another. By using 8- and 12-inch telephoto lenses and ultrasensitive color film, these dances were captured on film, and a few shots were made with still cameras. These were made from a blind located about 35 feet southeast of bower 1 and about 45 feet west of blind 2.

Bower 3 (a slender, nearly horizontal perch 35 inches high) was out of photographic range but well within earshot, and when birds went there to dance their motions were just discernible.

Bower 4, a slender sloping stick, heavily scratched, about 46 inches above ground, was frequently used. This bower was located behind thick bushes, which made it impossible to observe the dancing. However, from the persistent, rasping, insect-like sounds made during display, it was possible to keep track of the activities at this site also.

After prolonged observation, it appeared that one of these four bowers was the primary stage. This was bower 2 (which was later collected), where dances were most frequent and where the males maintained the most constant attendance. However, I noted that dancing males often moved from one stage to another. Because they occasionally did this when slightly disturbed by my movements, I suspected that such shifts had a defensive value. In other words, the series of

dance stages seemed to comprise alternate dancing places used by a group of male birds for the purpose of deluding predators. No sign of territorial defense was observed at any time, either on or about the bowers or in the trees overhead.

BREEDING SEASON

The Blue-backed Manakin was observed displaying strongly during the full period of observation—March 16 to 19, 1958. Spencer, who acted as guide, informed me that the birds normally displayed during this month—the hottest, driest period of the year, when streams dry up and forest fires do great damage, and when many of the deciduous trees, which provide a substantial portion of the forest cover, shed their leaves. This permits a great deal of light to penetrate to the floor of the forest at the season when the basal vegetation is used for dancing by *C. pareola*.

CALLS AND MECHANICAL NOISES

All observations relating to calls and mechanical noises were of birds on or within 20 feet of the bowers. The most wide-ranging call and the one most frequently heard above the dance grounds consisted of a kind of wren-like "wwwrrr," drawn out and ascending, and ending in an explosive "churr" or "chow," which was sometimes twice repeated.

This call was given by lone males perched 10 to 15 feet up in the forest. One male that the writer observed preened and frequently delivered this attention signal, with its head and bill pointed slightly upward and the throat bulged outward.

Late in the day, when activity abated, solitary males were seen to remain in and near the bowers, calling periodically. For example, at 1.10 P.M. on March 17, I wrote: "A male (blue) has remained in the vicinity [of bower 2] since 12.05 P.M. It calls periodically but often not for minutes at a time. Often the calls are answered in the distance. The answers are of the 'whee-whew' variety." Then a little later I wrote: "The male call is heard often. Frequently the wren-like 'wwwrrr' is heard without the 'chow,' or the latter may be repeated twice. This is the primary call."

The first call of the day was a short, descending "chew," followed quickly by an ascending, sweet, ringing whistle: "wheat." The two were delivered close together: "chewwheat." This call, which was apparently delivered by a lone male from a perch in the lower middle portion of the forest (about 20 feet up), was an invitation call. It was

sometimes varied with a call that I wrote as "chaa-chewchew." Another call that was heard often was a resounding phrase that rang through the forest like the clicking of billiard balls. I wrote it as "chu." This penetrating sound was rapidly delivered, three or four clicks to the second after an ascending series of whistled "kii's." This call was delivered by males as they gathered in the immediate vicinity of the dance stages or as they moved from stage to stage. Another call heard at this period was a mellower "whee-whew." Other calls that were heard near the bower began as "whee," then ascended to end in little churring rattles. These rattles and the noises next to be described may have been mechanical productions of the feathers.

The loud, undulating, insect-like buzzing mentioned above always accompanied the hopping and cartwheeling dances. The buzzing increased in tempo as the diameter of the cartwheel dance decreased, thus causing a more rapid flight pattern. Towards the end of these aerial gyrations the scraping sounds became very irregular and forced, as though they were purely mechanized sounds coming from a wavering toy top. Then the buzzing abruptly changed in nature, and the cartwheeling dance actually halted as one bird hovered and one bird landed on the perch. The hovering male then gave two to four rapid choking noises, with its mouth wide open and directed towards its dance partner, who now sat watching the widely gaping, hovering male.

TERRITORY AND MAKING THE DISPLAY GROUND

During the period of my observation, I saw no sign of territorial defense except one clash between an adult male and a young male, in which dancing partners changed twice during the course of a single cartwheel dance (see Excerpts from Field Ledger). But this observation was not supported by others.

The four territories in which the males danced were very limited in size. Each area was about 3 to 4 feet in diameter, and the dancing males never were seen less than 10 inches from the ground. There was no sign of ground clearing, and during the period of observation no manakin was ever seen on the ground below the perches, which was free of bushes. The dance perches themselves were bare of leaves, and many leaves about their perimeters bore many brown scars and blemishes as a result of constant stripping and pecking by the male manakins. Several times males were seen pulling at leaves with their bills, and twice they were seen with large segments of green leaf in their bills. These were carried to the dance stage and held in the bill

for a brief time before being disposed of. The clearing of an arboreal dance ground was heretofore unknown in birds except in the Magnificent Bird of Paradise (*Diphyllodes magnifica*; Rand, 1940, p. 8). In that species the dance ground is a vertical sapling in the deep forest around which the male owner clears a wide circle of earth. The Magnificent Bird of Paradise not only clears the ground debris beneath its display stage but rips off leaves on and above it. This clearing of arboreal leaves opens a kind of skylight window in the forest, and in this shaft of light the male displays his mirror-like ventral plumage, clinging breast up to reflect the light from the sky into the eyes of the female, which perches above him in display.

In the Blue-backed Manakin, the opalescent blue of the back and the red ornamental plumage of the crown, which extends backward in small, partially erectile horns, are probably enhanced by the increased light resulting from the reduction of leaves surrounding the bower.

Of course in this manakin, as well as in the Magnificent Bird of Paradise, the clearing away of leaves in the vicinity of the dance area may very well be primarily a defensive mechanism. These areas are frequented for many hours each day and for many weeks by both species of birds. It may be that the clearing away of leaves from the bower decreases the chance of successful attack by lizards, snakes, and even other birds, the ordinarily cryptic coloration of which would become revealing against a cleared background. In fact, any action on the part of these birds that tends to prevent or impede predators from lurking in concealment close to their habitually used dancing perches would seem to have selective value. In the case of the Magnificent Bird of Paradise, as well as the four species of six-wired birds of paradise (*Parotia*) that also clear the ground around their dance perches (the latter apparently do not clip away leaves), the clearing of the ground may very well be defensive. This seems likely in view of the fact that the male Magnificent displays while standing on a vertical sapling with his back horizontal to and only a few inches from the ground. While executing this dance he goes into a kind of trance and is undoubtedly more vulnerable to predators when in this state.

The author's observations of the display grounds of the Blue-backed Manakin and of various bower-building bowerbirds and birds of paradise indicate without question that these dance arenas attract predators. This being true, it is logical to expect that birds that have succeeded despite the handicaps imposed by constant threat of predators must have developed ingenious methods of defending themselves. The clearing away of leaves from arboreal perches as in *Chiroxiphia*

pareola and the clearing of ground arenas as in certain other manakins, birds of paradise, and bowerbirds may be convergent examples of the development of ingenious defensive mechanisms; and, indeed, the bower structure of the bowerbird may well have first arisen as a mechanism of defense.

In the Blue-backed Manakin one to four males were usually somewhere in the vicinity of the four dance areas. Solitary males often sat above or alongside the dance perches, and occasionally such males visited the perches to dance alone. At other times two males sat side by side on the main dance perch. There was an easy association between the adult male and the young male, with the two engaged in synchronized dancing activities. My observations indicated that the four dance arenas belonged to a group of males, the birds dancing at will in any of the four. However, arena 2 seemed to be the primary arena. Here the dances usually began and the widest variety of dances was performed. For example, it was only here that more than two males were observed performing together. Fortunately, my blind was situated so that I commanded a good view of two types of bowers, one with a nearly vertical perch (no. 1) and one with chiefly horizontal perches (no. 2). The bouncing parties consisting of up to four interacting males were seen only at the bower with horizontal perches. The cartwheel dances also were performed from these horizontal perches, but they resembled bouncing rather than cartwheeling because the upward hop was not possible except on the vertical stage.

Pairs of males occasionally left this bower to perform the vertical cartwheel in bower 1, which appeared to be a satellite or secondary dance arena.

REMARKS

The function of group dances between males is not clear. Apparently they are usually conducted with no female in attendance. Because of this it seems possible that the group displays between males serve to establish the hierarchy of the flock. It is perhaps significant that dances involving more than two males were always of short duration, and they generally ended with two males' hopping upward from the horizontal perches in a synchronized pair. This pair, which may have been the dominant pair of the group, then sometimes moved to an alternate bower to dance the vertical cartwheel. Perhaps it is significant that the latter varied from lengthy "spinnings" to short dances of 20 or so revolutions.

Thus it seems possible that in these birds the males establish their

position in the hierarchy of the flock by competitive dancing instead of by fighting, and that the most dominant males are the ones most likely to be chosen by the females. However, as mentioned above, females were never definitely seen in the dance areas, and copulation was never observed. Therefore, there is no direct evidence for this conclusion other than the fact that the males displayed socially and did not defend individual territories or fight among themselves.

For information concerning the reactions of these birds when a female is present, the reader is referred to the observations of D. W. Snow (1956, p. 90), who observed females as they joined the males on the main display perches. Snow reported that the males jumped up and down on each side of the female and that he once "watched one pair perform a joint dance in front of the female that was . . . perfectly coordinated." In another species (Dickey and van Rossem, 1938, pp. 336-337), the Long-tailed Manakin of Central America (*Chiroxiphia linearis*), the male is reported to leap back and forth over the female. Wagner (1945, p. 543) described such a dance and also one consisting of vertical leaps into the air. Furthermore, he observed the male to hover in the air facing the female, which remained passive.

Although he failed to observe a female, the present writer saw some patterns of courtship that had not been reported before. For example, the clan that he watched consisted of a group of males that split up to dance in pairs in any of a group of four dance arenas, whereas Snow (1956) found that individual pairs of males kept together much more closely. Also, many of the dances observed by the writer were between adult (blue and red) and young (green and red) males, with some of the performances even involving adult males and males so young that they were completely green except for a trace of red on the head. From these observations, it appears probable that the dances of the manakin are more complex than even Snow's remarkable observations suggested.

The writer was particularly impressed by the similarities existing between the dances that he observed in *C. pareola* and those reported for *C. linearis* by various observers. For example, Nutting (1884, p. 385) observed pairs of males performing the cartwheel dance that the present writer often observed in bower 1. Wagner (1945) described groups of males leaping from branch to branch, which the present writer observed only in bower 2. On the other hand, Slud (1957, p. 337) did not observe the type of dancing performed in bower 2, and in fact he seems to doubt its existence, for he wrote: "By no stretch of the imagination could this aery floating be interpreted as a leaping back and forth from branch to branch, a type of behavior I have never witnessed

nor ever been given cause to suspect in this species." However, Slud observed the cartwheel. He noted (1957, p. 338) that, although he had seen immature males dancing with each other in this manner, he never observed a mixed pair (an old and a young male), and that apparently the young males engage in courtship performances "only with other young males." This is certainly not the case in *C. pareola*, and, from the reports of Wagner, probably not the case with *C. linearis*. Therefore it seems possible that Slud and perhaps Snow observed only one form of the dance—the cartwheel. It may be significant that this cartwheel was the only form of dance that *C. pareola* performed when the observer was not concealed in a blind. In any event, both types of dances were observed in *C. pareola*.

EXCERPTS FROM FIELD LEDGER

MARCH 16

Landed Speyside at 2.30 P.M. Went to top of hill on Mr. Edbert Lau's plantation. Explored forest. By 5.00 P.M. had found *Chiroxiphia pareola* and built blind. By great good fortune a pair was displaying at about 4.45 P.M. when we crept into the area . . . a deep forested draw.

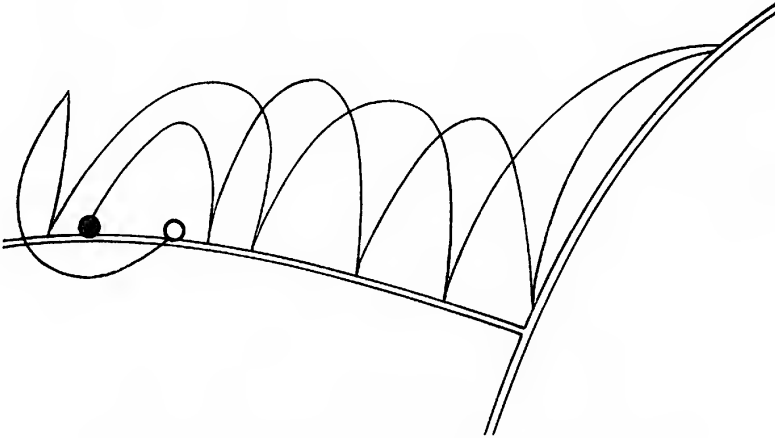


FIG. 2. Silent dance executed by a solitary adult male.

Dance: Two males, a blue-back and a green-back, circled as shown above [see fig. 2 from field ledger]. Bird A touched bent stick about 18 inches above ground, while other bird jumped and flew hoveringly upward and backward at B. In this vertical-hopping and backward-flying sequence the two birds windmilled while buzzing loudly. The buzzing was in cadence with the jumping.

MARCH 17

5.55 A.M. Enter blind.

6.14: The first manakin call: A clear, loud churring whistle, "kwii-kwii-cho," followed soon by other "kwii's" and a sharp, loud "cho-cho-cho."

6.14.45: Calls herald approach of birds, which descend to bower 1. Much buzzing on stage but no calls or songs. Many flurries of cartwheel dance, which is between a blue-and-red male and a green-and-red male. Blue-and-red male stops the cartwheeling flight to hover when green-and-red male ceases flying to perch on what would be the hub of the "wheel." Blue-and-red male hovers in front of perched green-and-red male and then flies out of sight.

6.20: Blue-and-red male returns to bower 1 from perch about 15 feet over and 20 feet away. Again cartwheels with a green-and-red male. The cartwheeling birds buzz loudly like insects. As these mechanical notes differ in sound on the upward and on the downward flights, the revolutions can be counted. During this performance I counted about 79 undulations of sound, indicating that each male went around the rim of the wheel about 40 times. Again the blue-and-red male flew the longest. It hovered in front of the green-and-red male, which was the first to break off the aerial gyrations by landing on the "hub." It sat there facing the blue-and-red male as it hovered momentarily facing it. After the blue-and-red male had departed, it flew to a low limb about 15 feet from the dance stage.

6.29: After a period of silence, sudden buzzing was heard at bower 1. Three dancers. Two green-and-red males and one blue-and-red male. These birds danced for one and one-half minutes. Each took turn. Magnificent. The blue-and-red male again hovered in front of the green-and-red male when it perched. The hovering bird seemed to choke momentarily with its mouth wide open, then it flew to a side limb to perch. Then one green-and-red male began hopping on the nearly vertical dance perch apparently alone, and uttering a sharp "qui-qui-qui."

6.35: At this time the party of manakins moved to a new bower area (no. 2), which the writer had not known of before. There they danced in various combinations. At 6.41, for example, two green-and-red males danced together. At the end of some 25 revolutions one hovered to "choke" in front of the other, which had landed. Just before this pair began dancing, three males (two green-and-red and one blue-and-red) hopped upward some four times in an alternating threesome, and then the blue-and-red flew to a perch 8 feet to the south to sit by while the two green-and-red males danced as above described.

6.45: A green-and-red male has been sitting on a perch 3 feet from bower 1 for four minutes. It sits with its feathers puffed out, and it is crouching on its perch as though sick or cold. Once or twice it gaped widely. The interior of the mouth seems unusually red.

7.01: Fifty-eight flurries between two green-and-red males, with a blue-and-red breaking into the cartwheel dance to replace one green-and-red male for 21 orbits. This was followed by the gaping display, after which the green-and-red male departed from the scene. The blue-and-red male thereupon began a silent bouncing display (fig. 2) which the writer had not observed before. It bounced from limb to limb like a slow-moving, feathery ball, moving in high, evenly rounded arcs.

7.16: An occasional sharp "qui-qui" from the trees over the bower. The dancing displays are entirely arboreal but seem to be conducted from stages that are within 2 or 3 feet of the ground. The birds under observation seem to be members of one clan.

8.12: The manakins are silent except for an occasional "wheat," emitted by a red-and-blue male, which resembles a sweet ringing whistle. A few minutes ago a blue-and-red and a green-and-red male visited bower 2, where, after some "buzzing," indicating dancing, the blue-and-red male disappeared and the green-and-red went to a perch 6 feet up and about 6 feet distant from the bower. It perched there silently, sometimes on one foot for more than a minute. Its quiet perching was suddenly disturbed by a call of startling shrillness emitted by a blue-and-red male from a low perch between bower 1 and bower 2. I happened to be watching the green-and-red male through 8-power glasses when this call was delivered. It actually made the bird jump as though frightened.

9.50: A blue-and-red male sat for half a minute on the horizontal perches of bower 2. When he went away, a green-and-red male flew down and sat on the same perch. Soon thereafter it began hopping and buzzing. In making pictures of this I apparently disturbed it with the camera motor, whereupon it flew to bower 3 (which at this time I had not yet discovered), where it continued its buzzing dancing.

10.03: A blue-and-red male landed on bower 2, where it hopped about alone emitting loud "chow" notes. Once it went to the side of the bower to pull at the foliage. It soon tore off a large piece of green leaf, which it then carried to the main display perch. There it sat with the leaf in its bill. Many of the leaves remaining around bower 1, which I examined yesterday, present a scarred, torn appearance. Earlier today another blue-and-red male brought a large section of green leaf to bower 2.

10.35: Magnificent dance of two blue-and-red males at bowers 2, 1, and 4. The pair moved "right down the line." A number of still photographs and 60 feet of film of these dances were exposed, using long lenses.

11.02: Have just watched a blue-and-red male as it perched on a limb 10 feet up and to one side of bower. It preened its tail, frequently emitting wren-like, ascending notes which ended in explosive "chow" or "chow-chow" notes. There is something about the latter that reminds one of the clashing of billiard balls. When these sounds are delivered, the bill is directed slightly upward and the throat is noticeably bulged. Another call of the red-and-blue male on his waiting perch is a "whee-phew."

In display the red crown feathers extend backward above the green feathers as do the ears of a shying horse.

Between 11.10 and 11.45 a blue-and-red male was continuously in the display area, and at 11.55 it visited the main stage of bower 2 and emitted the buzzing notes as it hopped or "bounced" up and down in solitude. This dance was filmed with 4- and 6-inch telephoto lenses.

12.05 P.M.: A blue-and-red male visited bower 2 and danced alone. (Twenty feet of film were exposed.) This male seems to make a habit of getting its red crown in the tiny shafts of sunlight that probe the bower area.

1.10: A blue-and-red male has remained in the vicinity of bower 2 since the last entry. It called periodically but often not for minutes at a stretch. Its calls were often answered in the distance.

2.30: A blue-and-red male has called frequently in the vicinity of the bowers. Some of its calls were wren-like and ended in explosive "chow's," but frequently the wren-like "wwwrrr" of the first part of the call was heard without the "chow," or the latter was repeated twice.

About 10 minutes ago I whistled a shrill ascending "whit-whit-wheat," and almost immediately a green-and-red male with its red crest partially expanded flew in and answered me. Further whistling on my part failed to attract other birds.

3.12: A solitary blue-and-red male landed on the center of bower 2, where it wiped its bill, turned, jumped a bit, and called "wheat" or "whit."

3.25: Mapped area, going to all four display arenas. The second one discovered centers on a 4-foot-long, nearly horizontal branch that is heavily scratched. This is the jumping stage where two blue-and-red males and two green-and-red males jumped together this morning.

4.35: Apparently no manakins in area since about 10 minutes ago. At 4.47 yesterday saw a dance very late in day. Today in the same place all is quiet.

4.55: Observations end.

MARCH 18

Observations were begun at 5.55 A.M. First manakin call, a "tuiet," was heard at 6.01 A.M. and repeated for a time every four or five seconds. The calls, which are loud, emanate from over bower 1. A manakin was seen fluttering almost bat-like from bower 3 to bower 1 and then back to 3. In the succeeding 12 minutes there was much calling, and at 6.20 a display began at bower 1, which the writer examined with care through 8-power glasses. [Figs. 4 and 5 were made from original field sketches of this display.]

At 6.21 A.M., following a shrill "wheat-wheat," a blue-and-red male and a green-and-red male flew to bower 1 and danced about 50 cycles (fig. 3). At the end of this dance the blue-and-red male choked as he faced the green-and-red male, which sat on the bower (fig. 4). Facing the young male at a distance of a few inches, it hovered with mouth wide open for about a second. Its flight reminded the writer of a crippled bird trying desperately to stay aloft. This male then flew to a perch 5 feet overhead, leaving the green-and-red male to hang on the near-vertical perch with one foot down and one up, like a grass warbler on a reed. The entire dance was apparently over by about 6.23 A.M., when the green-and-red male flew off in the direction of the blue-and-red male.

The dance is a vertical reverse cartwheel, with each bird performing exactly the same movements except at the end, when the blue-and-red male slows down and appears to lose control. At this stage his buzzing (and perhaps that of the young male as well) becomes more spasmodic, and he flies with his mouth wide open. It is then that the "cartwheel" turns slower and slower, and becomes smaller in diameter until the "wheel" halts altogether [at the position shown in fig. 4], with the blue-and-red male struggling to hover 4 to 6 inches from the head of the green-and-red male. [The foregoing was written after watching the dance through binoculars at a distance of 30 feet.]

6.40: A blue-and-red and a green-and-red bird arrived together at bower 2 and began their buzzing dance. This time I activated a stop watch (as well as the Arriflex) and found that the dance lasted for 1 minute 28 seconds, at the end of which time the adult male went through the aforementioned "chok-

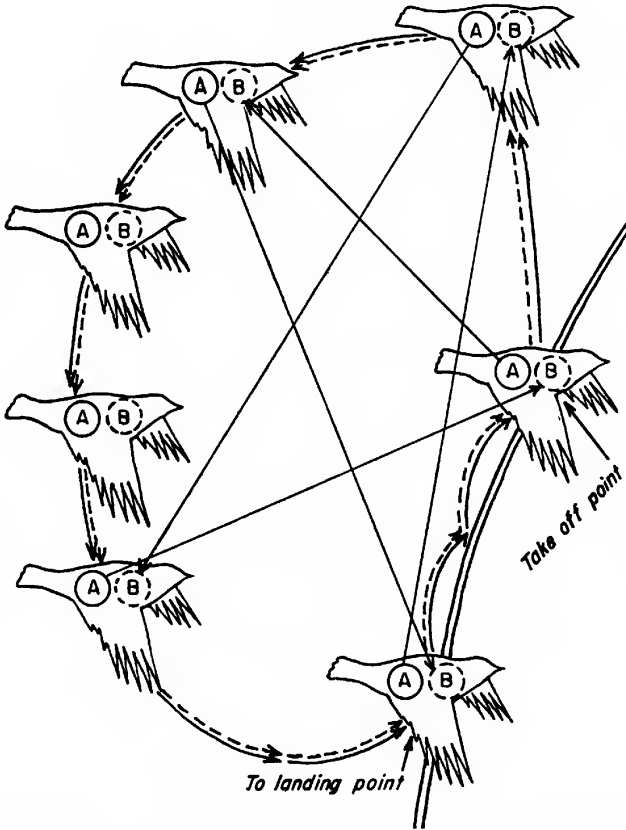


FIG. 3. Cartwheel dance. Reciprocating positions of the pair of interacting males (one adult and one subadult male) are indicated by the straight lines.

ing" ceremony, this time emitting a short, squeaky whistle just before it flew off.

At bower 2 at 6.46 A.M. two blue-and-red males and one or two green-and-red males arrived to dance. The two blue-and-red birds executed a cartwheel dance of about 30 convolutions. At first their hops were high and broad as they danced in the Y of the near horizontal main limbs, but, as the dance increased in tempo, the wheel effect or the hopping speeded up in cadence and the hops became shorter. [See fig. 3.] At 6.47.30 two adult males again danced at bower 2, with one or two green-and-red males sitting in the vicinity of the bower. At 7.06 a blue-and-red and a bird that on first inspection appeared totally green came to bower 2, where they danced exactly the same dance as that observed between the red-headed males. This dance [fig. 5] was watched through binoculars with no distraction from cameras or note taking. It lasted for less than two minutes. The green bird, which I had jubilantly taken to be an adult female, as this was the first all-green bird I had seen during many hours of observation, joined the blue-and-red male in the "cartwheel" dance, which, on the horizontal perches, looked more like bouncing. Their dance

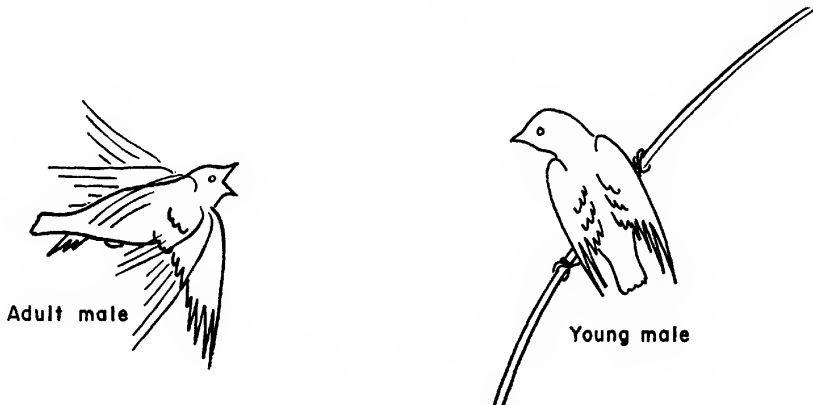


FIG. 4. At end of the cartwheel dance the adult male hovered for about a second (as shown), its mouth wide open as though gasping for air.

progressed from long, slow hopping accompanied by insect-like buzzing to short, speedy loops. This was followed by a halting, hovering flight, and then the blue-and-red male flew off and left the all-green bird. The latter remained a few seconds and then flew out of sight.

[On close observation of the "all-green bird," I noted a trace of rose on its crown. Later in the American Museum I examined a large series of *Chiroxiphia* and concluded then that this green bird was in fact a young male, probably in its first-year dress, and not a female.]

In cartwheeling or hopping both males were never hovering in the air at the same time, but they took off and landed simultaneously. The insect sound seemed to come from the throat, apparently forced out by the action of flying, so that it wavered in cadence with the wing beats. I noted that the throat was puffed out during flight, presumably indicating air pressure in the throat. [At the time this was written I was unaware of the fact that the primaries of *Chiroxiphia* are modified, apparently for the production of mechanical noises.]

I also noted that the red ornamental "horns" of the blue male are elevated and expanded during periods of display. The most unusual aspect of the performance between the all-green male and the red-and-blue male was the fact that halfway through the dance a red-headed green male intruded (cut in) and actually danced with the all-green and the blue-and-red bird. This dance lasted about 15 seconds and consisted of about 30 flurries. With three birds dancing, the arena of the dance widened, and I saw the all-green fly at the red-and-green male from perch A to position B. It appeared to fly directly at the intruding red-and-green male as though to attack it head on. However, there was no physical encounter, and immediately after this feint it dropped to position C and continued to dance with blue-and-red. The last part of the dance consisted of all-green dancing with blue-and-red, red-and-green having left the scene.

Later in the day these events took place: 8.40 A.M., bower 3, buzzing indicating a dance; 9.07, bower 4, buzzing indicative of a dance; 9.55, an extended

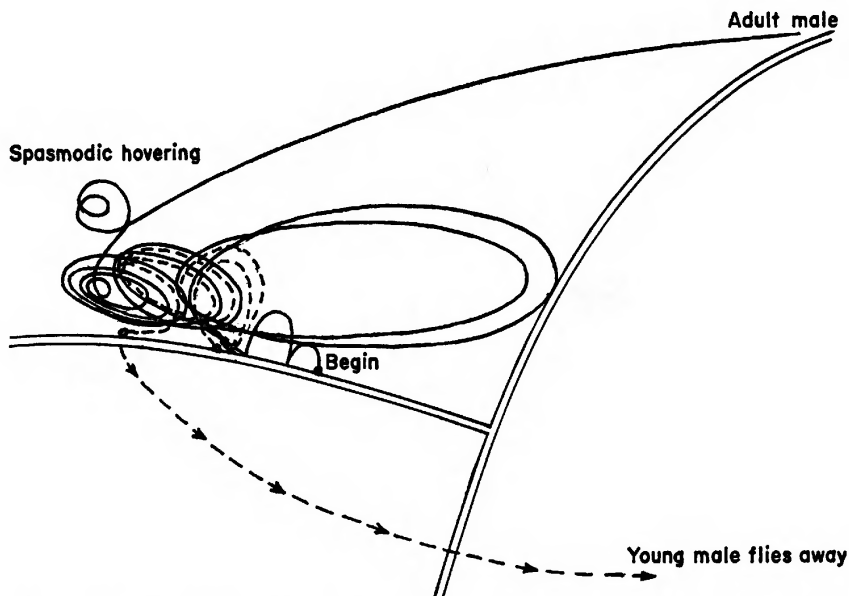


FIG. 5. Dance between a young male (all green except for a trace of rose on crown) and an adult male.

dance of perhaps 60 cycles at bower 4; 10.03, a small dance at bower 1; 10.08, dance began at bower 4, and, as soon as it finished, one male flew from there to bower 2, where it began a buzzing dance.

10.11: At about this time I had the good fortune to film a blue-and-red male and a green-and-red male. The pair dropped into bower 1, where they immediately began a cartwheel dance. Having waited some 20 hours for this dance to occur when the light was right for photography, I was elated to capture the scene on 60 feet of film. The two males cartwheeled about 25 feet from my blind as I filmed the dance with an 8-inch telephoto lens. This dance consisted of the vertical cartwheel motions described for the other dances executed at bower 1.

This day there were buzzing dances at 10.10 A.M. at bower 2; a dance of about 67 flurries at 10.40 at bower 3; then a dance at the same bower involving some 29 cartwheels.

Earlier on this morning (at 9.40), as I was about to record the presence of a small blue butterfly flying in a shaft of sunlight in the vicinity of bower 1, I was startled to see a Blue-backed Manakin slip silently down to this same bower and sit on its main upright limb. It remained silent and moved very little as the butterfly flew nearby, its blue closely matching the blue of the manakin's back. It was probably more than coincidence that the blue-backed male dropped down to this display area when the blue butterfly appeared near the bower. The records show that this bower was rarely visited by solitary birds.

At 11.50 A.M., just before preparing to depart, I placed a green plant with a red flower in the center of bower stage 2. A blue-and-red male saw the flower and moved actively through the foliage 10 feet above ground, then it sat in various places half-concealed, giving wren-like calls and weak "wheat" or weak "chow" notes.

At noon a short buzzing display was heard at bower 4. At 12.53 P.M. the observations ceased. Close-up photographs were then made, and the main bower (no. 2) was collected for reassembly in the American Museum. Although we had cut and packed bower 2 in its entirety, at 1.50 P.M. a pair of males began their buzzing dance at bower 4, which was out of sight but only about 30 to 50 feet from where we noisily worked at folding canvas and so on.

MARCH 19

On the morning of March 19 the writer returned briefly to the area where these observations were made. Males were heard displaying in the draw, apparently undeterred by the missing bower. This is one reason for postulating that the alternate dance stages act as a defense mechanism.

SUMMARY

The courtship displays of a clan of Blue-backed Manakins (*Chiroxiphia pareola*), observed in 1958 on Tobago Island, are described. Two forms of dancing were found: (a) a vertical cartwheel dance involving two males, which seemed to persist until one of the males became too fatigued to dance any further; and (b) a "bouncing" dance involving one to four males, in which the birds bounced lightly back and forth (often over each other) on nearly horizontal limbs. The cartwheel dances were executed by mixed pairs of males of various ages ranging from the nearly solid green young male and the red-crowned green subadult to the blue-backed, red-headed adult.

The clan of manakins was observed dancing in four bowers located in a line close to the ground in tall second-growth forest. One of these bowers seemed to be the primary dancing area. None of the bowers was defended, and none was the private dancing stage of a particular male or pair of males. Instead, the bowers were used seemingly at random, the pairs of males resorting to them to dance the cartwheel dance when, for unknown reasons, they chose to desert one of the other bowers, even in the midst of a dance. This shifting of arenas is postulated to be a mechanism of defense to offset the actions of predators attracted by the dances.

Ecology, mechanical noises, calls, and bower building are described. The last consists of a leaf stripping around the bowers. Reference is made to leaf stripping in the Magnificent Bird of Paradise (*Diphylodes*) and to the clearing of the ground in certain other bower-making

birds. It is postulated that the clearing away of arboreal and terrestrial leaves and debris may also be a mechanism of defense, as it almost certainly tends to reduce the protective value to predators of their cryptic coloration. Social dancing between males in these highly polygamous manakins is thought to function as a replacement for fighting in the selection of the dominant breeding stock.

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